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GILL DEVELOPMENT IN MYTILUS.[1]

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In the present paper no attempt is made to give an exhaustive treatment of the subject; the intention is rather to summarize briefly the work that has been done upon the development of the lamellibranch gill, and to describe somewhat fully certain phenomena in the development of the gill of *Mytilus* which seem thus far to have escaped notice. A few incidental observations on gill development in other lamellibranch genera are added.

Terminology.

The term ctenidium is used in the following pages to designate the entire respiratory apparatus of one side of the body. The halves of each ctenidium are called, in accordance with common though questionable usage, the gills, outer and inner respectively according to position adjacent to the mantle or to the body mass. Each gill, again, is composed of two lamellæ, called respectively the direct (or descending) and reflexed (or ascending). The same terms are employed in describing the limbs of the filaments composing the lamellæ. It will be noticed that the reflexed lamellæ (and filament limbs) of the outer and inner gills are turned in opposite directions — that of the inner gill toward the body, that of the outer gill toward the mantle. The *Mytilus* gill is of a very simple filibranchiate type in which the interfilamentary connections (between neighboring filament limbs of the same lamella)

[1] The studies upon which the present paper is based were carried on largely in the Marine Biological Laboratory, Woods Hole, Mass., and the Harpswell Laboratory, South Harpswell, Me. I am happy at this opportunity to express my appreciation of the courtesies and assistance extended by the directors of these institutions, Professors C. O. Whitman and J. S. Kingsley, and by their associates.

are represented solely by tufts of interlocking cilia, the ciliated disks (Fig. 7, *B*, *a*). The interlamellar connections are also very simple, consisting of hollow, cylindrical bridges, several of which extend between the two limbs of each adult filament (Fig. 7, *B*, *b*).

Résumé of Previous Investigations.

The classic on the development of the gill in the Lamellibranchiata is the paper by Lucaze-Duthiers ('56) entitled "Mémoire sur le développement des branchies des mollusques acéphales lamellibranches." A preliminary report ('54) preceded it. The first anlage of the ctenidium is described as a row of papillæ arising inside the mantle, along the line of juncture of mantle and body. These lengthen, bend back upon themselves, and become the filaments of the inner gill. Later a second series of similar papillæ form just outside the first, and develop similarly into the outer gill. Each gill thus passes through a stage in which it is composed of a row of unbent filaments hanging down in the mantle cavity.

The work of Lucaze-Duthiers was preceded by two interesting papers by Lovén ('49), in which young bivalves of several species are described and clearly figured with the ctenidium consisting of from three to ten free filaments belonging to the inner gill. The material was obtained from the plankton; and the identification (*Mya*, *Tellina*, *Mytilus*, *Mactra*, and *Nucula* are hesitatingly named) was recognized as very questionable by Lovén himself. Moreover, little account of the development is given.

Since the time of Lovén and Lacaze-Duthiers the investigation of gill development has been extended to a considerable number of widely separated genera of lamellibranchs.

Early stages of *Cyclas* were studied by O. Schmidt ('54); and his work on this genus has been extended by Leydig ('55), Stepanoff ('65), and Ziegler ('85), while Lankester ('75) gives brief notes on the closely allied genus *Pisidium*.

Unio and *Anodonta* have been described by Braun ('78), Schierholz ('78, '89), and F. Schmidt ('85).

The earliest stages of the gill of *Teredo* have been described briefly, and not very clearly, by Hatschek ('80). Sigerfoos ('96) has confirmed the observations of Hatschek and extended them to much later stages.

Ostrea has been briefly considered by Ryder ('84) and Stafford ('05).

Mytilus has been equally briefly described by Wilson ('87).

Dreissensia is known through the work of Korschelt ('91), Weltner ('91), and Meisenheimer ('01).

And, finally, the gill development of the peculiar and primitive Nuculidæ, *Nucula* and *Yoldia*, has been very carefully followed by Drew ('99, '01).

The accounts are for the most part brief, in some cases only incidental; and there are various points of divergence in detail. One such divergence appears at first to be fundamental. While Lacaze-Duthiers describes the first anlage of the gills as a series of isolated papillæ, the majority of the authors cited trace the ctenidium back to a longitudinal fold or ridge, which is secondarily constricted transversely and divided into the papillæ. Thus emphatically, among later writers, Ziegler for *Cyclas*, Schierholz for *Unio*, and Sigerfoos for *Teredo*. Drew describes a primary ridge and secondary papillæ in the Nuculidæ, but considers the change to be "due to unequal growth more than to constriction"; his figures, however, give evidence of considerable constriction.

On the other hand, Wilson confirms the early view of Lacaze-Duthiers for *Mytilus*; and my own observations are entirely in accord with this view. Concerning *Dreissensia* Korschelt ('91, p. 144) expresses himself thus cautiously: "Ob sie (the gills) in Form einer Falte angelegt werden, die sich schon sehr bald einkerbt und so jene vermeintlichen Papillen entstehen lässt, oder ob sie als wirklichen Papillen hervorsprossen, ist schwer zu entscheiden."

In the adult of all forms a continuous and undivided gill axis may be recognized, comparable with this embryonic fold or ridge. Upon this are carried the filaments, comparable with the embryonic papillæ. The whole divergence, then, reduces itself to a question of the relative time of development, and is one of minor importance. Much more significant is the general uniformity of development, and the recognition, by all the authors cited and in all the genera studied, of a stage in which each ctenidium is represented by a series of simple papillæ belonging to the inner gill; and of a later stage in which the outer gill is formed of a parallel series of corresponding papillæ.

Concerning the process of elongation and flexure by which the embryonic papillæ are metamorphosed into the definitive filaments of the adult gill in all forms except the very primitive Protobranchia the authors are again in the fullest agreement, so far as their attention has been turned to this later development; and this plan of development has been generally accepted as characteristic of the whole class.

Stages of Gill Development in Mytilus.

The following tabulation gives the size of the animal and the number of filaments present in the gills at certain of the more important stages in gill development. The figures can be taken only as approximate, as there is considerable individual variation; but they probably represent fairly accurate averages as they are selected from a much larger tabulation.

Stage.	Size.	Number of Filaments.	
		Inner Gill.	Outer Gill.
Earliest stage in which gills were observed.	0.30 mm.	3	0
Flexure of filaments of inner gill.	0.75 mm.	12	0
First appearance of outer gill.	1.40 mm.	20	(?)[1]
Flexure of filaments of outer gill.	1.60 mm.	25	15

Order of Succession of Gill Filaments In Mytilus.

Lacaze-Duthiers describes the order of the development of the filaments of the inner gill as from front to back, the most anterior being the first to develop; in the outer gill the development is described as extending in both directions, so that the first developed filaments would come to lie in the middle of the gill, with late developed filaments at both ends. My observations are in accord with those of Lacaze-Duthiers as regards the inner gill; but, in the case of the outer gill, amendment is required.

In very early stages, in which the filaments of the outer gill are mere papillæ, the longest papilla is not the most anterior, but is even posterior to the middle of the series. In one specimen with ten such papillæ, the seventh from the front is the

[1] Theoretically but a single filament should be present. No stage has been actually observed with less than three or four. Apparently several filaments appear almost simultaneously.

longest, the most developed, and, apparently, the oldest. Lacaze-Duthiers figures an almost exactly similar stage ('56, Fig. 6), as well as one a little older ('56, Fig. 7) in which the ninth of fifteen filaments is the longest. This suggests strongly a development of the gill in both directions in the early stages.

On the other hand, a comparison of these early stages with others much older shows that the position of the anterior end of the outer gill is somewhat definitely located relatively to the inner gill. There seems to be some individual variation; but the extension of the inner gill in front of the outer is measured in all cases observed by about ten filaments. Owing to the non-parallelism of the filaments of the two gills, it is very difficult to interpret figures that have not been drawn with reference to this particular point; but a study of Lacaze-Duthiers's plate seems to show ten such filaments in an earlier stage ('56, Fig. 6) and eleven in a later ('56, Fig. 7). As the inner gill is growing only at the posterior end, and as the filaments of the two gills are arranged somewhat definitely in corresponding pairs, this indicates almost certainly that the addition of filaments at the anterior end of the outer gill is confined to very early stages, if present at all. As regards these early stages my observations are very inconclusive.

In this connection it is also interesting to note that in a comparatively early stage, when the animal is only about 1.60 mm. in length and the outer gill is composed of only about sixteen filaments, the anterior filament of this gill is already strongly differentiated from its neighbors in both size and shape. It is decidedly thicker and longer, and is furnished with a very peculiarly enlarged and twisted termination. In both total preparations and sections it is very distinct from the other filaments and very easily identified. From this time on the development of the outer gill is clearly from front to back only, and the two gills develop *pari passu*.

Mode of Formation of Later Filaments in Mytilus.

The early filaments of the *Mytilus* gill follow the mode of development so beautifully worked out by Lacaze-Duthiers, and outlined briefly above; the later filaments follow a very different

mode. The change may be noticed in specimens but a little older than the latest stage figured by Lacaze-Duthiers. The ctenidium has grown beyond the rather small body mass and the posterior adductor, and extends free into the mantle chamber (Fig 1). The posterior part of the ctenidium is free from the mantle except for a light attachment due to the interlocking of

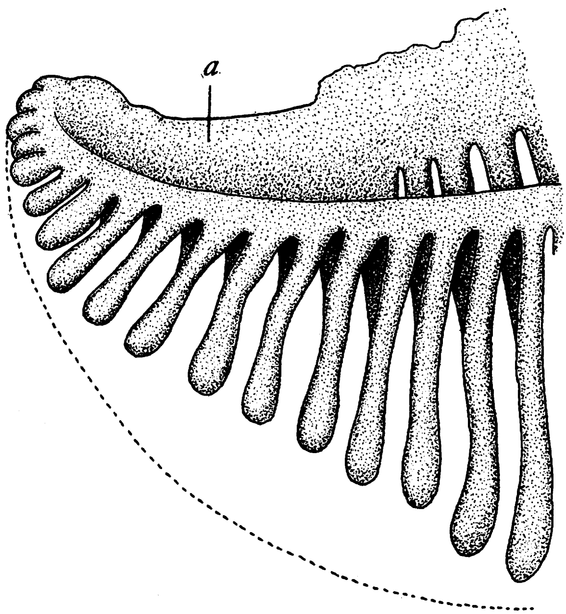

FIG. 1. Posterior tip of ctenidium of *Mytilus* of 2.5 mm. length, viewed from inner side. Outer gill omitted except for outline represented by dotted line. Magnification 170.

cilia. This suggests the connection of neighboring gill filaments (interfilamentary connections); but here there is merely diffuse ciliation and no specialized ciliated disks.

At the posterior end the gill axis (Fig. 1, *a*) is slightly curved upward; and around this curved end the developing filaments are closely crowded and assume a radial arrangement. The anterior filaments are attached to the ventral side of the axis and hang down ventrally; toward the end the position becomes more and more oblique, and then horizontal; while the youngest filament anlagen actually project upward from the dorsal side of the axis. Here all stages in filament development may be observed, ar-

ranged accurately in serial order. In Fig. 4 are seen isolated portions from the posterior end of the ctenidium. The specimens figured are selected from a large number of dissections, and are taken from several individuals of slighty varying size. Hence the discrepancy in the size of the figures, as all are equally magnified. All the stages figured have been observed again and again.

From the figures it is clearly seen that we are dealing with something very different from the comparatively long and slender

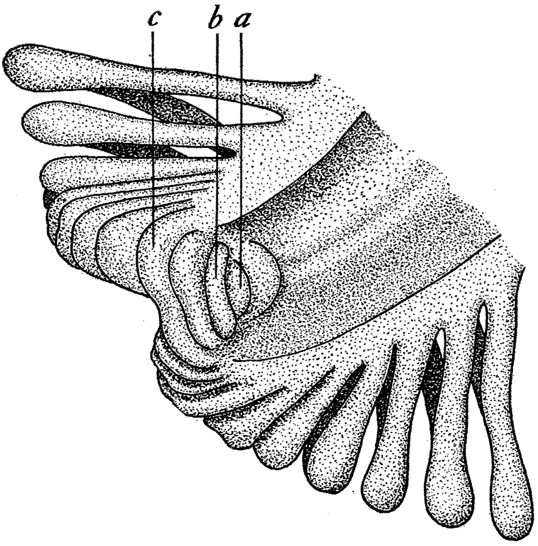

FIG. 2. Posterior tip of ctenidium of *Mytilus* of 3.0 mm. length, spread out, and viewed from dorsal side. Inner gill below and to right. Magnification 170.

rod-like papillæ observed in younger specimens. The youngest anlagen are rather transverse folds or ridges on the dorsal and posterior sides of the gill axis. At first these ridges are comparatively short and of uniformly convex contour (Figs. 4, *A*; 2, *a*; 3, *a*). Then the ridge elongates and becomes flat topped (Figs. 2, *b*; 3, *b*); and soon a process of differential growth or constriction leads to a notching of the ridge near its middle (Figs. 2, *c*; 3, *c*; 4, *B*). This notch divides the originally simple anlage into two slightly unequal parts, the larger belonging to the outer gill and the smaller to the inner. These two parts grow rapidly

(Figs. 4, *C*; 4, *D*), and may be followed readily into the characteristic filaments of their respective gills (Figs. 2 and 3).

In this connection it should be strongly emphasized that the filament anlagen here described are by no means the equivalent of the papillæ described by Lacaze-Duthiers, although their appearance in such a stage as that figured in Fig. 4, *D*, is strikingly similar. The undivided transverse fold (Fig. 4, *A*) contains potentially an entire filament of each gill; and each of its subdivisions (Fig. 4, *D*) is the equivalent of the two limbs of a filament placed side by side. On the other hand, the earlier type of anlage must be considered as the equivalent of only one limb of the definitive filament, or perhaps better, of the two placed end to end. In the earlier type the reflexed limb of the filament originates through a bending of the anlage; in the later type there is no bending, but rather a longitudinal splitting. The exact details of this splitting and the formation of the cavity within the gill, shown in Fig. 4, *E*, have not been worked out; but a study of a series of specimens such as those represented in Fig. 4 makes it clear that the process consists essentially in a thinning and ultimate perforation of the plate-like anlage of Fig. 4, *D*.

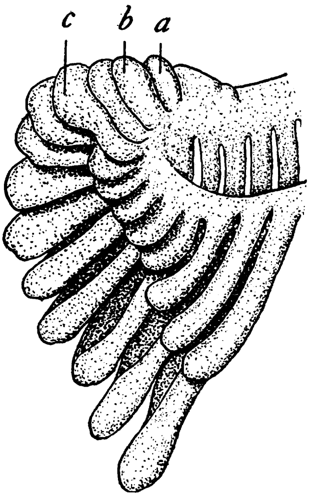

FIG. 3. Posterior tip of ctenidium of *Mytilus* of 4.5 mm. length, viewed from inner side. Magnification 170.

Corroborative evidence as to the nature of these later filament anlagen and their distinction from the earlier and more anterior ones is found in the character of the ciliation. A comparison of Figs. 4 and 5 is instructive in this connection. Fig. 5 is drawn from a section; but the filaments of the gills have been slightly reconstructed from neighboring sections, so that they are represented in their entirety. This represents an earlier filament of the outer gill (Fig. 5, *b*), with its characteristic rod-like form. Details of the ciliation have been omitted except for the some-

what diagrammatic representation of the highly specialized ciliated epithelium characteristic of the outer side of the filament, *i. e.*, the side turned away from the cavity of the gill. Thus in the inner gill (Fig. 5, *a*) the outside of each limb of the bent filament shows this characteristic ciliation ; the papilla, or unbent filament, of the outer gill is ciliated on only one side, and that the side corresponding to the outside of the direct limb. In the later filaments (Fig. 4) the conditions are very different. In the

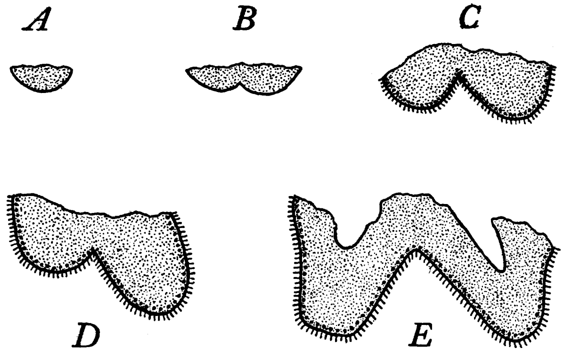

FIG. 4. Isolated filament anlagen from posterior tip of ctenidium of *Mytilus*. In all cases, anlage of outer gill at right. *A* and *B* from specimen of 2.25 mm. length ; *C* from one of 2.00 mm. ; *D* from one of 2.30 mm.; *E* from another specimen of 2.25 mm. Magnification 140.

two youngest stages represented (Figs. 4, *A* ; 4, *B*) the tissue is distinctly embryonic with no differentiation ; but in the three older stages (Figs. 4, *C* ; 4, *D* ; 4, *E*) the ciliated epithelium is clearly distinguishable, and is located on both sides of the anlage, showing the equivalence of the latter to both limbs of the flexed filament.

Another difference between early and late filament formation is found in the relations of the upper end of the reflexed filament limb. In the earlier filaments, the reflexed limb, developed at the free end of the direct limb, is primarily free. In *Mytilus* it retains this freedom ;[1] but in many lamellibranchs the upper ends of reflexed filament limbs are secondarily fused with the

[1] Even in *Mytilus* there is a fusion of the upper ends of the reflexed filament limbs with one another to form a somewhat definite border to the reflexed lamella of the gill.

mantle (outer gill) or body (inner gill). In the later type of development the upper end of the reflexed limb is primarily united with the gill axis (Fig. 4, *D*), and only secondarily attains its freedom. The details of the process have not been studied. In the specimen represented in Fig. 4, *E*, this separation had not taken place, but the reflexed limbs were torn loose in the dissection as indicated by the rough edges.

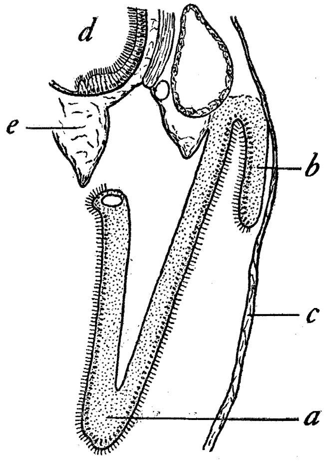

FIG. 5. Section through ctenidium of *Mytilus* of 1.6 mm. length. Section passes through posterior end of reduced foot. *a*, filament of inner gill; *b*, filament of outer gill; *c*, mantle; *d*, intestine; *e*, foot. Magnification 140.

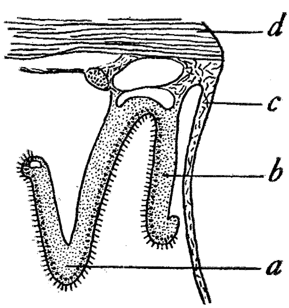

FIG. 6. Section through ctenidium of *Mytilus* of 1.6 mm. length. Section passes through middle of posterior adductor. *a*, filament of inner gill; *b*, filament of outer gill; *c*, mantle; *d*, posterior adductor. Magnification 140.

At first sight the two modes of filament formation seem fundamentally distinct; but the change from one to the other is bridged by all intermediate gradations. A comparison of Figs. 4, 5, and 6 gives some suggestion of the transition in the case of the inner gill; and the process is identical for the outer gill.

Figs. 5 and 6 are taken from the same animal, Fig. 6 being more posterior, thus showing a later filament in a younger stage of development. But it will be found by measurement that the ratio of the length of the reflexed limb to the direct limb of the filament of the inner gill is almost the same in the two cases, thus showing a precocious flexure of the posterior filament. A

further advance in this precocity leads to the condition found in a still later filament (Fig. 4), in which the flexure may be considered as having already occurred at the time when the filament is first budded forth.

Thus it is possible to conceive the later method of development as derived from the earlier; but it is equally possible, so far as mere geometrical relations are concerned, to reverse the series and consider the later mode as really primitive, the earlier mode as a specialization. It may be that the feeding requirements of the young animal are such as to require an adaptive modification in the direction of a speedy lengthening of the gill filaments; but it is likewise possible that the later mode of development is an adaptation to some factor or combination of factors in the life of the older animals. The startling similarity of the anlage of the later filaments to the gill in young specimens of the very primitive *Nucula*, as figured by Drew ('01, Fig. 46) make it very tempting to interpret the later type as primitive; but the structures are in such undeveloped condition that such comparisons are hazardous. The safe course is a suspension of judgment.

Filament Development in Other Lamellibranchs.

In connection with the above observations on *Mytilus*, the gill development in various other forms has been hastily studied for comparison. *Mya* is the only genus in which very young specimens have been observed. Here the early development seems to agree essentially with Lacaze-Duthier's description of *Mytilus*. Later stages have been studied in *Mya*, *Anomia*, *Modiola* and *Arca*. In all these genera the development of the later filaments follows the scheme here set forth for *Mytilus*. It is highly probable that this modification of development is characteristic of the later filaments in the Lamellibranchiata in general.

Development of Interlamellar Connections in Mytilus.

The contrast of the interlamellar connections in the closely related genera *Mytilus* and *Modiola* has been emphasized in a former paper ('98). In *Mytilus* these connections (Fig. 7, *B*, *b*) are irregularly cylindrical, and each contains a large blood cavity communicating with the cavities in the two limbs of the filament.

There are several such bridges between the limbs of each filament in a well-grown specimen. The particular filament figured had three interlamellar connections; but other filaments of the same animal showed four. In *Modiola*, on the other hand, the filament limbs are united by a continuous membrane (Fig. 7, *A*, *b*) which extends from the point of flexure for more than half the length of the reflexed limb. Sectioning shows that this membrane is composed of a very loose connective tissue with abundant blood spaces. The question immediately arises which of these types of connection is to be considered primitive. On other grounds than gill structure the view was expressed in a former paper ('98) that *Modiola* is the more primitive form. In that connection the *a priori* argument was advanced that the *Mytilus* type of gill filament might be easily derived from the *Modiola* type, while an independent origin of the interlamellar bridges of *Mytilus* would be more difficult to conceive.

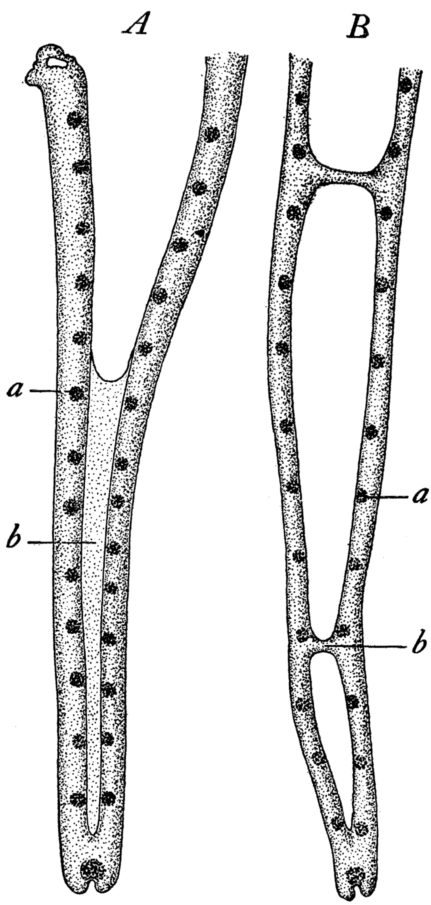

FIG. 7. Filaments of adult gill of (*A*) *Modiola* and (*B*) *Mytilus*. Only a part of *Mytilus* filament represented. *a*, interfilamentary connection (ciliated disk); *b*, interlamellar connection.

The examination of the development of these bridges confirms this view. Fig. 8 shows, in outline, the tips of five consecutive filaments of the gill of *Mytilus*. The filaments are arranged in the order of their occur-

rence in the gill; but the order of developmental stages is not the same. In the latest stage (Fig. 8, *E*) an interlamellar connection is present at a considerable distance from the tip of the filament; in the next younger stages (Figs. 8, *A*; 8, *C*) the connection is found nearer and nearer to the tip of the filament. Finally, in the earliest stage (Fig. 8, *B*), there is no distinct connection; but the distance through which the two limbs of the filament are in union at the tip as compared with the much shorter distance in Figs. 8, *A*; 8, *C*; or 8, *E*, shows a potential interlamellar connection in an undeveloped condition. The comparison with the

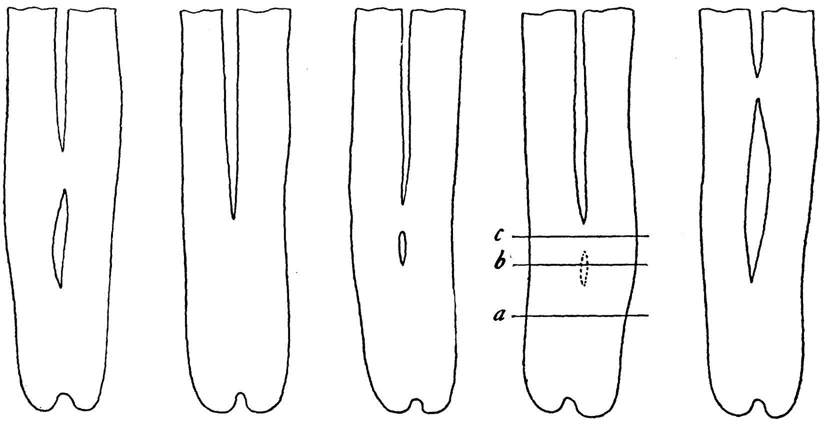

FIG. 8. Tips of five consecutive filaments of inner gill of *Mytilus* of 6 mm. length, showing formation of first interlamellar connection. Filaments represented in order of occurrence in gill; order of developmental stages of interlamellar connection is *B*, *D*, *C*, *A*, *E*. Magnification 110.

continuous connecting membrane of *Modiola* is evident, and it is hardly going too far to call this a "*Modiola* stage" in the development of the filament of *Mytilus*.

Perhaps the most interesting stage in the development of the interlamellar connection is shown in Fig. 8, *D*, which shows clearly the mode of formation of the *Mytilus* type of connection from its *Modiola*-like anlage. The filaments shown in Fig. 8 were first studied and sketched as total preparations, then sectioned. The study of the total preparation indicated that the area bounded by dotted lines in Fig. 8, *D*, was not an opening

like that separating off the interlamellar connection in the other filaments. The appearance was rather that of a thinner spot or constriction preliminary to complete perforation. Study of the sections fully confirmed this interpretation. In Fig. 9 three such sections are represented, their positions being represented by light horizontal lines in Fig. 8, *D*. The section nearest the tip (Fig. 9, *A*) shows a direct connection between the cavities of the two

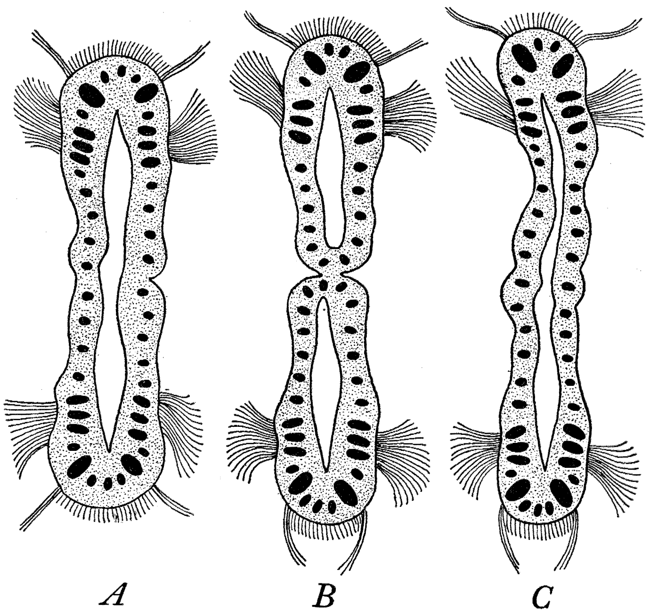

FIG. 9. Transverse sections of filament represented in Fig. 8, *D*. Position of sections shown by horizontal lines in Fig. 8, *D*, marked with corresponding letters. Magnification 540.

filament limbs in the neighborhood of the edge of the gill. Corresponding sections of other filaments show the same arrangement. The section farthest from the tip (Fig. 9, *C*) shows an essentially similar arrangement, which is duplicated by sections through the interlamellar connections of the other filaments. In the intermediate section (Fig. 9, *B*) the gill filament is strongly constricted, and the connection of the cavities of the two limbs is entirely interrupted. The next stage would be a complete perforation in place of this constriction, and the local separation of the filament limbs. Three successive degrees of such separation are shown in Figs. 8, *C*; 8, *A*; and 8, *E*.

Development of Interlamellar Connections in Other Lamellibranchs.

All stages in the development of the interlamellar connections in *Mytilus* have been repeatedly observed; but the investigation has not been extended to other genera. The similarity of the structure of the interlamellar connections in certain other forms, *e. g.*, *Astarte*, suggests similarity of development. But in the majority of the lamellibranchs the structure of these connections resembles *Modiola* rather than *Mytilus*.

General Conclusions.

There is a very striking parallel in *Mytilus* between the formation of the interlamellar connections (p. 71) and the separation of the two limbs of the later gill filaments (p. 68). In each case a flat, plate-like organ becomes locally thinner and is finally perforated. The parallel may be extended, though less fully, to the separation of the upper ends of the reflexed limbs of these later filaments from the gill axis (p. 70). As regards the two latter processes, at least, the parallel has been further extended to embrace several other widely divergent genera (p. 71), and is probably capable of general application. Moreover an essentially similar process may be recognized in the formation of slits in the primitive gill fold, as described by Hatschek ('80) and Sigerfoos ('96) for *Teredo*, and by Ziegler ('85) for *Cyclas*. The general process of perforation or separation in gill development appears to be of very common occurrence among the lamellibranchs.

The opposed process of fusion is equally characteristic. In the *Mytilus* gill this process is reduced to a minimum, but it may be noted in the fusion of the ends of the reflexed filament limbs. Other forms, however, show a high degree of fusion in the development of complicated inter-filamentary connections, represented in *Mytilus* by the simple ciliated disks; and an entirely different type of fusion has been noted in a former paper ('00) as occurring in certain of the complexly folded gills.[1] And, finally,

[1] This paper has been criticised by W. G. Ridewood ("On the Structure of the Gills of the Lamellibranchia," *Phil. Trans. Royal Soc. London*, Ser. 3, Vol. 195, 1903), who holds that the phenomena there described should be interpreted as the result of a splitting of filaments, not a fusion. I see no reason to change my previous view. As regards the present argument, splitting, like fusion, would indicate plasticity of the gill.

in many genera there is a more or less extensive fusion of the reflexed lamella of the outer gill with the mantle and of the inner gill with the body mass, or, posteriorly, with the corresponding lamella of the other ctenidium.

The frequency and prominence of these two opposed processes in development strengthen the conviction earlier expressed ('98) that the lamellibranch gill is an extremely plastic organ and one very liable to adaptive modification. This being the case, it is not an organ of fundamental phylogenetic importance, and has been given an altogether undue prominence in recent classifications of the Lamellibranchiata.

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